

## Scaling in Nests of a Social Wasp: A Property of the Social Group

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**Abstract.** The numbers of brood cells in nests built by founding swarms of the Neotropical social wasp *Polybia occidentalis* closely correlate with the numbers of wasps in the swarms. We analyzed nests of different sizes to determine how they scale with respect to the allocation of brood cells among combs. Three patterns were evident: compared to smaller nests, larger nests have (1) more combs and (2) larger combs; and (3) among nests containing the same number of combs, the last two combs diverge in relative size as nest size increases. Taken together, these results suggest that members of a swarm somehow “know” the size of the swarm they are in. This information feeds back to individual builders, which quantitatively modulate their responses to stigmergic cues in ways that result in the nest-size-scaled allocation of brood cells among combs. The patterns also suggest that swarms fine-tune the final size of their nests by making corrections as they build.

### Introduction

The process of nest construction by a social wasp colony does not differ fundamentally from nest construction by a solitary wasp. In each case individuals construct the nest by executing a series of discrete innate building acts. Each act adds to the nest one new load of material, oriented in response to cues intrinsic and extrinsic to the nest. As far as we know, in no social insect species do individual workers specialize only in certain kinds of building activity over

their lifetimes. That is, every individual in the colony possesses the full repertory of acts required to build the nest. Thus, even the most complex nests of colonial species could, in principle, be constructed by a solitary individual working alone, given enough time. To the extent that this is true of the social wasps, it argues that the broad, species-typical form of the nest does not depend on properties of the group or on processes such as self-organization, but is simply the result of the additive contributions of individual actions by individual actors. In this view, the construction process is directed by a mechanism in which builders respond to stimuli arising from the structure of the nest. Interactions among builders are only indirect, mediated by the structure they are cooperating to build, a mechanism referred to as stigmergy (Grassé, 1959; Theraulaz and Bonabeau, 1995; Camazine *et al.*, 2001).

But are there any patterns in the nest of a social species that are under the more direct influence of the social group? Here we provide evidence that the answer is yes. We show for a swarm-founding social wasp, *Polybia occidentalis* (Olivier), that nests of different sizes scale in ways that point to a quantitative modulation of the building rules in response to feedback about the size of the swarm.

### Nest Construction in *Polybia*

*Polybia occidentalis* is a Neotropical wasp whose nesting behavior has been described in some detail (Forsyth, 1978; Jeanne, 1986, 1996). Colony-founding swarms comprise a small number of queens and a large number of workers. As a swarm arrives at the nest site it has chosen, a few workers immediately begin constructing the first downward-oriented, hexagonal cells. These are attached directly to the substrate, typically a twig. As more cells are added radially, the developing comb takes on a discoid form, extending freely from both sides of the twig. As the comb grows, there is space for increasing numbers of workers to become

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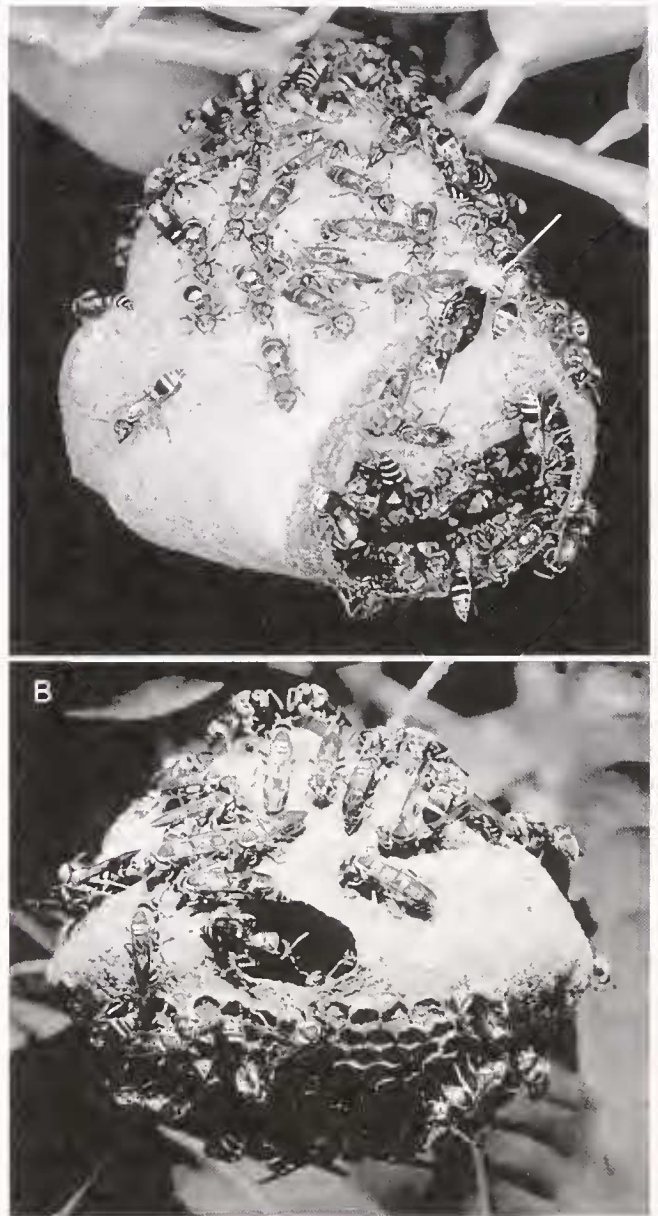
engaged in building. Meanwhile, the queens begin laying eggs in the cells.

When the first comb reaches a certain size, the builders' behavior makes a qualitative shift (*qualitative stigmergy*; Camazine *et al.*, 2001). Instead of adding more cells to the edges of the comb, workers begin extending the outer walls of the peripheral cells downward and outward to initiate the envelope, starting at the back and sides of the comb. As this sheet grows, it is warped toward the center to form a domelike covering about 2 cm below the comb (Fig. 1A). The envelope is not completely closed, however; a 1-cm opening is left in the front to provide an entrance to the comb. Then in the reverse qualitative shift, the second comb is immediately begun, the walls of its cells being drawn downward from the lower surface of the envelope just completed. This comb is expanded from the center (bottom) of the supporting envelope outward toward its margins (Fig. 1B). A new envelope is constructed over it in the same manner as the first. Then the next comb is begun in the same way. The alternation between construction of combs and envelopes continues until the nest is large enough to house the adult wasps of the swarm and the brood they will rear. The entire construction process typically takes a week to 10 days. The nest remains at this size for many weeks or months; thereafter, enlargement occurs episodically (Wenzel, 1993; AMB, unpubl. data).

Thus the nests of *P. occidentalis* are modular, each module consisting of a comb and its envelope. Swarms work in complete modules: each comb + envelope module is constructed to its final size before the next one is begun, and it is rare for a founding swarm, once it starts a new comb, to leave it half-finished or uncovered (RLJ and AMB, pers. obs.).

*P. occidentalis* swarms vary widely in size, yet each is able to construct its nest with a number of cells that correlates closely with the number of wasps in the founding group (Forsyth, 1978; Jeanne and Nordheim, 1996). A similar pattern is seen among founding groups of *Polistes* (Wenzel, 1996). The size of the nest built by the swarm may well optimize the trade-off of opposing costs such that colony output is maximized. On the one hand, if the swarm builds too few cells, it will not have the space to house the brood it is capable of rearing, and the subsequent rate of colony growth will be limited. On the other hand, if the nest is much larger than required to house the brood population, forager mortality may be high due to the extra foraging demands for nest material, leaving too few workers to rear the brood efficiently (O'Donnell and Jeanne, 1992).

The form the nest takes is a function of two sets of decision processes engaged in by individual builders in the colony. One is the decision by a worker as to what kind of building act to engage in. *P. occidentalis* workers perform three primary kinds of building acts: brood-cell-wall construction, envelope construction, and surface thickening for



**Figure 1.** Nests of *Polybia occidentalis* under construction. (A) Envelope construction. The envelope covering comb 3, whose cells are visible inside, is nearing completion. The rim of dark material is recently added carton, still wet. As more material is added to the envelope edge, the opening will be constricted to form the new entrance to the nest, just below the current entrance (line). The greatest width of the nest is about 6.5 cm. (B) Comb construction, frontal view. The nest entrance, center, opens into the space between comb 2 and its envelope, which forms the bottom of the nest. Comb 3, its cells exposed on the lower surface of the envelope covering comb 2, is expanding outward with the addition of new cells. When the cells reach the angled edge of the envelope, their outer walls will be extended downward and outward to initiate envelope 3, beginning at the back of the nest. Note the campanulate shape of the nest. The greatest width of the nest is about 5 cm.

reinforcement of the upper nest walls (Jeanne, 1986). The second set of processes has to do with the orientation of the material being added to the nest during a particular kind of

Table 1

Descriptive statistics for the *Polybia occidentalis* colonies used in the study

Component	Mean	Median	SD	Range	<i>n</i>
Adults	476	355	399	24–1,802	80
Nest cells	1,360	1,050	1,154	109–7,152	85
Nest combs	3.9	4	1.2	2–8	85

All colonies were initiated by absconding swarms. Data were collected after 25 days of pre-emergence-stage development.

building act. The most important orienting cues are stigmergic, that is, come from the nest itself (Grassé, 1959; Camazine *et al.*, 2001), and it is the innate response to these that determines the species-typical nest form. Gravity is an important external orienting cue.

We investigated the influence of group size on workers' responses to the stigmergic orienting cues that determine the allocation of cells among combs. We did this indirectly by measuring nests built by different sizes of swarms in Guanacaste, Costa Rica. (For details about the site and methods, see Jeanne and Nordheim [1996] and Bouwma *et al.* [2000].) Combs were numbered sequentially from the top of the nest, in order of construction. We define the size of the  $i^{\text{th}}$  comb in terms of the number of brood cells,  $C_i$ , it contained, and the size of the nest in terms of the total number of brood cells,  $C_t$ , in all combs.

The 85 nests used in the study covered a 65-fold range in size, while the number of combs per nest,  $m$ , ranged from 2 to 8 (Table 1). For the analyses of patterns in scaling, nests of 2–5 combs were used ( $n = 78$ ); the sample size of nests of 6–8 combs was too small to analyze ( $n = 7$ ). Three patterns were evident in the scaling of nests. We describe these in order of their salience.

#### Larger nests have more combs

Not surprisingly, larger nests contained more combs than did smaller ones, although there was considerable overlap in size between nests of  $m$  and  $m + 1$  combs (Fig. 2). The distribution of the number of combs,  $m$ , in the nest as a function of nest size,  $C_t$ , fits a power function with the equation

$$m = 0.335C_t^{0.351}.$$

This relationship implies that each new comb was larger than the preceding one. This is seen more clearly in a plot of the number of cells in each successive comb (Fig. 3). The data fit the first-order linear regression equation

$$C_i = -156.6 + 192.4i,$$

where  $i$  is the ordinal number of the  $i^{\text{th}}$  comb in the nest. Thus, each new comb,  $i$ , had on average 192 more cells than

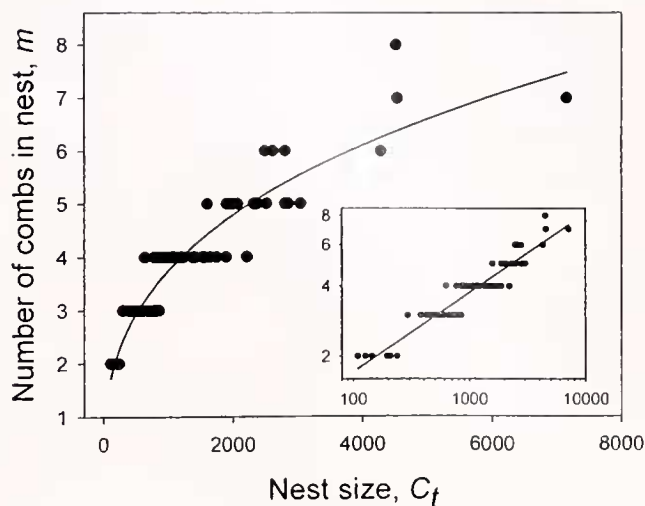


Figure 2. Number of combs in swarm-constructed nests of *Polybia occidentalis* as a function of the total number of cells in the nest. The fitted regression is the power function,  $m = 0.335C_t^{0.351}$  ( $r^2 = 0.89$ ,  $n = 85$  nests). Inset shows same data plotted on log-log axes with a fitted linear regression. Linear regression equation:  $\text{Log } m = -0.45 + 0.34 \log C_t$  ( $r^2 = 0.90$ ).

the preceding one,  $i - 1$ . Because the number of cells in a comb is proportional to the comb's area, while the comb's diameter increases as the square root of its area, the constant absolute increase in cell number from comb to comb gives the nest a campanulate shape (Fig. 1B).

#### Larger nests have larger combs

The second pattern is that combs of larger nests were larger than the corresponding combs of smaller nests (Fig. 4). This pattern held both within the set of nests with the

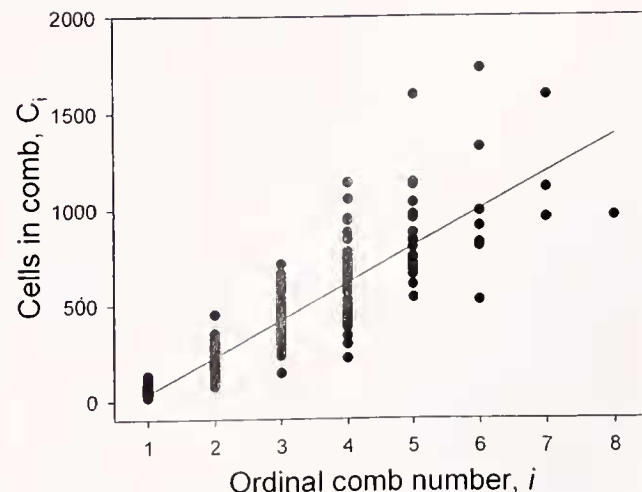
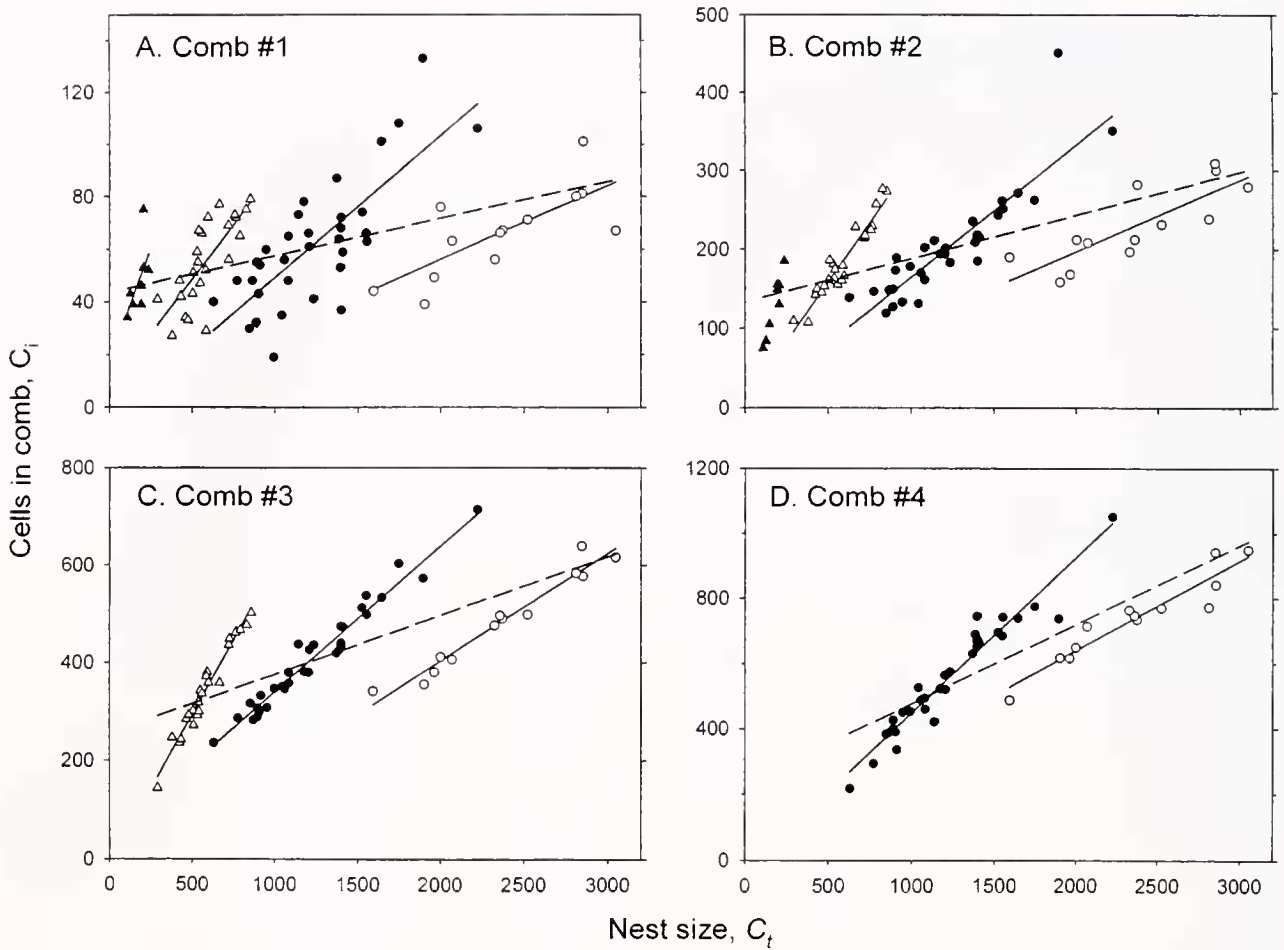


Figure 3. Comb size by ordinal comb number. The equation for the regression line is  $C_i = -156.6 + 192.4i$  ( $r^2 = 0.80$ ,  $n = 85$  nests).



**Figure 4.** Distributions of sizes of individual combs as a function of overall nest size. Each graph plots sizes of combs of the indicated ordinal comb number. (A) Comb 1; (B) Comb 2; (C) Comb 3; (D) Comb 4. Within a graph, each plot is of nests of the same total comb number,  $m$ : solid triangles:  $m = 2$  (i.e., 2-comb nests); open triangles:  $m = 3$ ; solid circles:  $m = 4$ ; open circles:  $m = 5$ . For all regression lines shown,  $P < 0.001$  (regression for comb 1 in 2-comb nests:  $P = 0.11$ ). Solid lines represent linear regression equations for nests of the same comb number,  $m$ : (A)  $m = 2$ :  $y = 16.76 + 0.17x$ ,  $r^2 = 0.37$ ;  $m = 3$ :  $y = 6.87 + 0.08x$ ,  $r^2 = 0.58$ ;  $m = 4$ :  $y = -5.07 + 0.05x$ ,  $r^2 = 0.60$ ;  $m = 5$ :  $y = -0.08 + 0.03x$ ,  $r^2 = 0.55$ . (B)  $m = 2$ :  $y = -16.76 + 0.83x$ ,  $r^2 = 0.93$ ;  $m = 3$ :  $y = 7.71 + 0.30x$ ,  $r^2 = 0.91$ ;  $m = 4$ :  $y = -3.91 + 0.17x$ ,  $r^2 = 0.77$ ;  $m = 5$ :  $y = 15.31 + 0.09x$ ,  $r^2 = 0.66$ . (C)  $m = 3$ :  $y = -14.58 + 0.62x$ ,  $r^2 = 0.96$ ;  $m = 4$ :  $y = 42.55 + 0.30x$ ,  $r^2 = 0.96$ ;  $m = 5$ :  $y = -38.64 + 0.22x$ ,  $r^2 = 0.95$ . (D)  $m = 4$ :  $y = -33.57 + 0.48x$ ,  $r^2 = 0.93$ ;  $m = 5$ :  $y = 84.35 + 0.28x$ ,  $r^2 = 0.90$ . Dashed lines represent fitted linear regression equations for all data in each graph (i.e., comb  $i$  for all nests): (A) Comb 1:  $y = 43.5 + 0.01x$ ,  $r^2 = .25$ ,  $n = 78$ . (B) Comb 2:  $y = 133.1 + 0.05x$ ,  $r^2 = 0.43$ ,  $n = 78$ . (C) Comb 3:  $y = 254.5 + 0.12x$ ,  $r^2 = 0.58$ ,  $n = 70$ . (D) Comb 4:  $y = 230.2 + 0.24x$ ,  $r^2 = 0.73$ ,  $n = 46$ . Note that the scale of the y axis increases in the graphs from A through D.

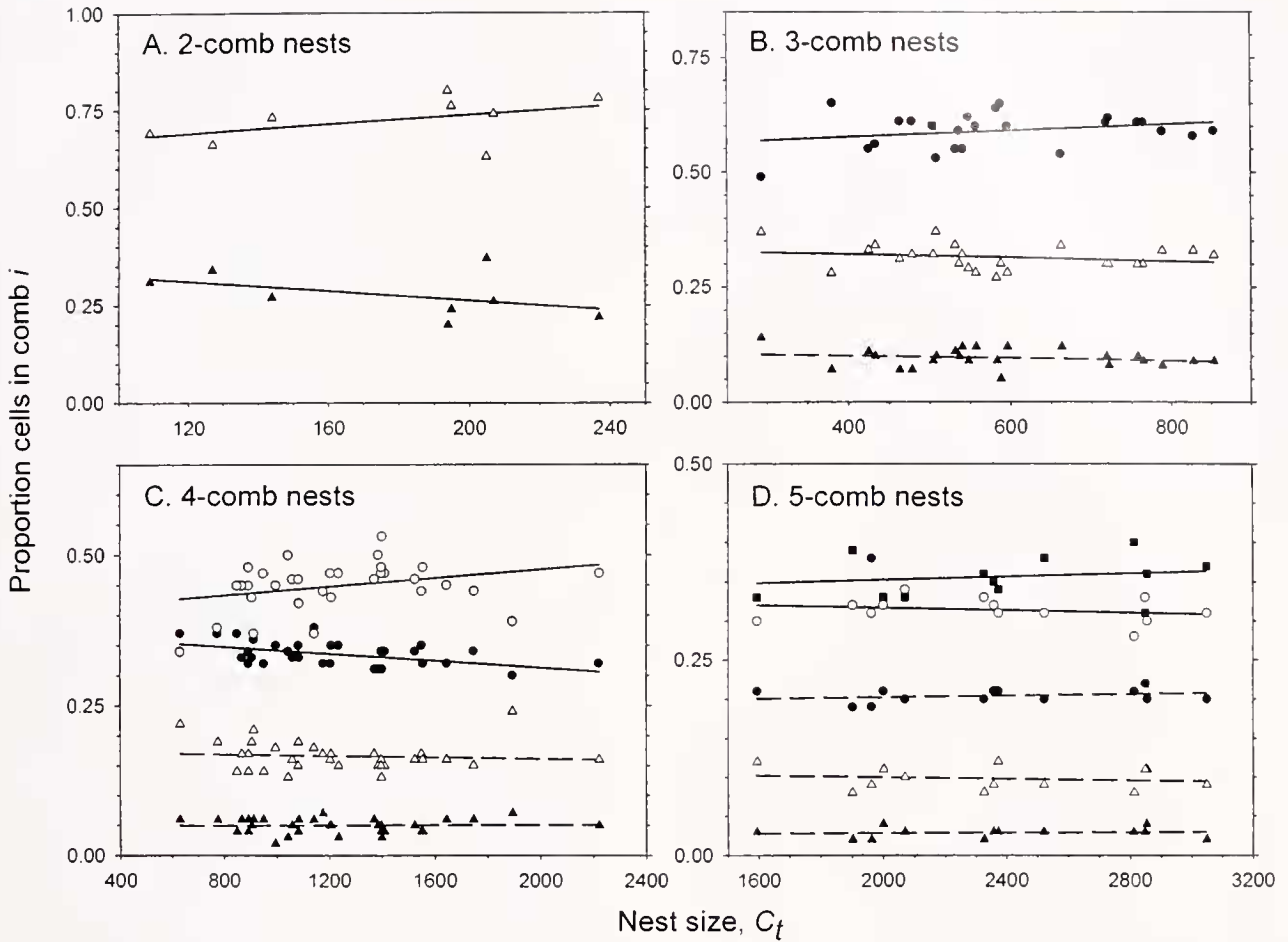
same number of combs,  $m$ , (Fig. 4, solid regression lines) as well as across the set of all nests of 2–5 combs (Fig. 4, dashed regression lines).

*Among nests of  $m$  combs, the last two combs diverge in relative size as nest size increases*

The third pattern is the least clear-cut, but is worth noting nonetheless. Within each set of nests of a given number of combs ( $m$ ), the proportions of cells in combs  $m$  vs.  $m - 1$

tended to diverge as nest size increased (Fig. 5). Although the slope of only one regression differed significantly from zero (comb 3 of 4-comb nests) and the slopes of the regression lines for the last and the next-to-last combs differed significantly from each other only for 4-comb nests, for all four sets the slope of the regression of cells in comb  $m$  on total cells in the nest was positive, but that of comb  $m - 1$  was negative.

The number of combs in the nest depends on how individual builders respond to the choice, "Now that the envelope is complete over comb  $i$ , do I initiate cells of comb  $i +$



**Figure 5.** Proportion of cells in the nest in each comb,  $i$ , as a function of nest size, by nests of a given comb number. (A) 2-comb nests; (B) 3-comb nests; (C) 4-comb nests; (D) 5-comb nests. Solid triangles:  $i =$  (comb) 1; open triangles:  $i = 2$ ; solid circles:  $i = 3$ ; open circles:  $i = 4$ ; solid squares:  $i = 5$ . Lines are fitted linear regression equations: (A)  $i = 1$ :  $y = 0.38 - 0.0006x$ ;  $i = 2$ :  $y = 0.62 + 0.0006x$ . (B)  $i = 1$ :  $0.11 - 0.00003x$ ;  $i = 2$ :  $y = 0.34 - 0.00004x$ ;  $i = 3$ :  $y = 0.55 + 0.00007x$ . (C)  $i = 1$ :  $y = 0.05 + 0.000008x$ ;  $i = 2$ :  $y = 0.17 - 0.000007x$ ;  $i = 3$ :  $y = 0.37 - 0.00003x$ ;  $i = 4$ :  $y = 0.40 + 0.00004x$ . (D)  $i = 1$ :  $y = 0.03 + 0.000001x$ ;  $i = 2$ :  $y = 0.11 - 0.000005x$ ;  $i = 3$ :  $y = 0.19 + 0.000005x$ ;  $i = 4$ :  $y = 0.33 - 0.000008x$ ;  $i = 5$ :  $y = 0.33 + 0.00001x$ .

I or do I quit?" Given the correlations between swarm size and nest size (Jeanne and Nordheim, 1996) and between nest size and number of combs reported here, the conclusion that group size influences this decision is inescapable. As a rule, once a founding swarm initiates a new comb, it completes it and covers it. However, the occasional observation of a few unfinished cells exposed on the lower envelope of a completed nest hints at variation among individuals with respect to their threshold of response to the cue (or cues) that stimulates initiation of a new comb.

The size of a comb under construction is determined by the switch from expanding the comb to constructing its envelope. The later this decision is made, the larger the comb. It is clear from our data (Fig. 4) that the switch is made later by swarms building larger nests. Since combs

$i > 1$  are built on the envelope of the preceding comb, part of the input into the decision to switch may be stigmergic. As these combs are expanded from the center of the domed envelope, each successive cell is built on a surface whose angle is increasingly divergent from horizontal. The cue that the switching rule uses may include this angle. Comb  $i = 1$ , on the other hand, is just a shelf of cells extending into space, providing far less in the way of potential stigmergic cues as to when to switch to construction of the envelope. Yet this comb also increases in size with nest size (Fig. 4A), suggesting that a larger swarm builds a larger first comb using no information other than the size of its own group.

The third pattern gets at the question of when, during the course of constructing the nest, the final nest size is set. Does the swarm "know" from the start of construction how

large a nest it will build, or does it make corrections as it goes? Three observations suggest that the latter is the case. First, whereas the correlation between the size of combs 1 and 2 is relatively strong ( $r = .83$ ;  $n = 85$ ), the correlation of comb 1 with later combs progressively weakens. The ability of comb 1 to predict the overall nest size is not very good ( $r = .46$ ). Second, the amount of variance in comb size that is explained by nest size increases with comb number,  $i$  (Fig. 4,  $r^2$  values increase, A–D). Third, there is substantial overlap in size among nests of  $m$  and  $m + 1$  combs, especially for nests of  $m > 2$  combs (Fig. 2; Figs. 5B–D), suggesting that swarms adjust final nest size by deciding whether to add a final module. The overlap is probably due to variation in the sizes of the first few combs built by swarms of similar size. Consider, for example, two swarms, each of which will ultimately build a nest of 2000 cells. Nests of this size may have four or five combs (Fig. 2). If swarm A builds combs 1–4 smaller than average, it will build a 5th comb, but this final comb will not need to be much bigger than comb 4 to achieve the total of 2000 cells in the nest (see Fig. 5D). On the contrary, if swarm B builds combs 1–3 larger than average, then it will get the 2000 cells by adding one more comb, but that comb will have to be disproportionately larger (see Fig. 5C). The nest of swarm A is toward the low end of the size distribution of 5-comb nests, while that of swarm B is toward the high end of the size range of 4-comb nests. The combs of nest B will average 25% larger than those of nest A. As Figure 5 shows, however, most of this average difference in proportions tends to be absorbed by the last comb.

Taken together, these observations suggest that swarms fine-tune the final size of their nests in the later stages of construction. Thus, although comb 1 aims roughly in the direction of the ultimate nest size, the trajectory toward the final nest size is guided en route, rather than ballistically following from comb 1.

### Conclusions

The construction of a nest by a social insect colony involves the performance of a set of behavior patterns that vary in species-specificity and evolutionary age (Wenzel, 1996). Some may be invariant across higher taxa. The use of the mandibles to manipulate nest material, for example, is universal among social Hymenoptera and Isoptera and apparently pre-dates the evolution of sociality in both groups. The rules by which nest material is applied in response to stigmergic cues from the nest also vary in their taxonomic breadth.

At one extreme, tactile feedback *via* the antennae is used to center construction of a shared cell wall between opposite walls of two adjacent brood cells and to determine the size of the cells (West-Eberhard, 1969). This is an example of the use of the body as a template to produce the regular hexagonal pattern of the comb. This building rule probably

varies little if at all among species of social wasp, except in the interesting case of the Vespinae, where the queen builds worker-sized cells, and the workers (which are smaller) build both worker- and queen-sized cells.

At the other extreme are species-specific rules—those that result in the nest architecture characteristic of a species. In our view, there is little evidence that the resulting patterns in nest structure at any of these levels are emergent properties of a self-organizing process. Rather, they appear to be largely the products of quantitative and qualitative stigmergy (Camazine *et al.*, 2001).

At the intraspecific level, however, things may work differently. The evidence we have presented clearly indicates that *Polybia occidentalis* swarms are able to allocate brood cells among combs so that size and number of combs scale with swarm size. What mechanism could give rise to this pattern? Several previous studies have suggested ways that groups of social insects might build their nests to a size that accommodates them. One possibility is that the mass of the swarm itself serves as a template to adjust the size of the nest to the size of the swarm. This appears to play a role in construction of the two-dimensional nests of *Leptothorax* ants (Franks *et al.*, 1992; Camazine *et al.*, 2001). Swarms of *Metapolybia* wasps build nests of single combs on a flat surface. A ring of “guards” is arrayed around the comb as it is constructed (Forsyth, 1978). If the guards are a fixed proportion of the swarm, then expanding the comb to the ring could produce a nest of the right size. But use of such a template cannot explain the scaling patterns seen in *P. occidentalis*, whose three-dimensional nests are extended into open space below a supporting twig, while the bulk of the swarm remains clustered to the side on the twig.

A related idea is that construction stops when the nest is large enough to house the swarm (Camazine *et al.*, 2001). In its simplest form, this mechanism would predict that comb size would be constant across swarm size and that larger swarms would simply build nests with more combs. It does not explain our observation in *P. occidentalis* that the scaling of the nest to swarm size begins with the first comb and continues throughout construction.

A third possible mechanism is that cells are constructed to keep up with the oviposition rate of the laying queens (Deleurance, 1950; Camazine *et al.*, 2001; but see Wenzel, 1996). Again, this mechanism cannot be working in *P. occidentalis*, because cells are built at a rate that well outpaces the collective rate of oviposition by the queens in the swarm (RLJ and AMB, pers. obs.).

A fourth possibility is that self-organization plays a role. However, there is no evidence that the scaling of the nest proportions by a particular swarm is an emergent pattern arising at the colony level from interactions among workers, nor is there any apparent involvement of positive feedback in the process.

None of these mechanisms adequately explains our re-

sults. Likewise, stigmergic cues, although important, are clearly insufficient alone to account for the swarm-size-dependent patterns we see among nests. Instead, we suggest the following mechanism. All three of the scaling patterns we describe for *P. occidentalis* indicate that information about group size flows from the group to the individual builders. We suggest that the quantitative rules governing the details of nest size and proportions in response to stigmergic cues are plastic and are modulated by group size. Although nothing is yet known about the building rules or stigmergic cues used by *P. occidentalis*, the following hypothetical example illustrates how this mechanism might work. The size of a comb may be determined by a rule according to which a builder decides between adding another new cell at the periphery of the comb being constructed and beginning the envelope for that comb. The quantitative set point for such a rule apparently differs according to whether the builder is in a large or a small swarm. A possible stigmergic cue in this case is the angle of the surface of the envelope on which the cells are being built. The first cells in the comb are built in the center of the envelope, that is, where the envelope's curved surface is tangent to a horizontal plane, or  $0^\circ$ . Because the envelope is domed, as the comb expands radially across the surface of the envelope, each new cell is built at a steeper angle from the horizontal than the previous cell (Fig. 1B). Thus, the behavioral rule in the context of a small swarm might be, "If the angle at which the current edge of the comb is  $\geq 25^\circ$ , then begin building the envelope instead of adding another cell." We suggest that in a large swarm, this quantitative set point may be nudged up to, say,  $30^\circ$  in response to information about swarm size fed back to the builder from the group. This change would result in a comb's being larger when being built by a large swarm than when built by a small swarm. Because the envelope subsequently built over the larger comb would also be larger, the increased size would propagate itself throughout the remaining modules of the nest. In other words, we are hypothesizing that information about group size modulates the quantitative set points of the rules of response to stigmergic cues.

In conclusion, we see little evidence that self-organizing processes play a role in nest construction in *Polybia occidentalis*. Rather, construction of the species-typical features of the nest can be understood as quantitative and qualitative stigmergic mechanisms, wherein cues from the nest structure at each stage of construction provide information to the builders as to what building act to perform next, where to perform it, and how to orient the addition of the new material. In accomplishing these tasks, individual workers interact only indirectly, *via* the structure of the nest (Camazine *et al.*, 2001). We have provided evidence that changes in nest proportions accompany changes in swarm size. We argue that these patterns cannot be explained by stigmergy alone, but appear to involve direct communication, no doubt

through cues, of information about the size of the group. In response, builders subtly modulate their responsiveness to quantitative stigmergic cues so as to yield the appropriate nest proportions. Although the mechanisms by which group-size information is transferred to, perceived by, and acted upon by individuals are unknown, there is little evidence that a self-organizing process is involved.

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